

PRIMARY AND SECONDARY SEED DISPERSAL OF A RARE, TIDAL WETLAND ANNUAL, *AESCHYNOMENE VIRGINICA*

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Abstract: Seed fall from the parental plant and subsequent dispersal by tidal water flow were investigated in *Aeschynomene virginica* (sensitive joint-vetch) in order to understand how these processes may affect local population regeneration and inter-population seed exchange. Local seed fall was estimated using seed traps around four isolated plants. Plots enclosed on all four sides by mesh fences were compared to plots with the streamside open to examine seed dispersal by water flotation. Seed flotation times and stream flow rates were then used to estimate the potential for water dispersal of seeds after they have fallen to the soil. Ninety-four percent of all seeds fell within 0.5 m of maternal plants, with an exponential decrease in dispersed seeds with distance from the base of parental plants. More seeds left open plots than completely enclosed plots, but there was no difference between the number of seeds leaving plots that had standing vegetation and those without vegetation. At least 50% of the seeds placed in water remained floating after 28.4 hours, and 5% remained floating after 81.8 hours. Water flow rates in wetlands where *A. virginica* occurs naturally may carry seeds over 2600 m from the maternal plant, representing a significant potential for water dispersal of seeds in this species. Seed movement out of patches may impact population dynamics of the patch from which the seeds leave. Dispersing seeds cannot contribute to the population in that patch the following season. Seed dispersal may also represent an important mechanism for a species such as *A. virginica*, which specializes in open, newly created habitats, to find and colonize new habitat patches.

Key Words: hydrochory, plant conservation, primary dispersal, rare plant, secondary dispersal, tidal wetland

INTRODUCTION

Seed dispersal in flowering plants represents a key process in the regeneration and establishment of plant populations. Seed dispersal patterns play important roles in 1) the number of new individuals added to a population (Schupp and Fuentes 1995), 2) the spatial arrangement of individuals within a local population (Schupp and Fuentes 1995), 3) the potential to establish new populations in suitable habitat patches (Hanski and Simberloff 1997), and 4) the degree of genetic interconnectedness among different populations (Waser et al. 1982, Gornall et al. 1998, Cain et al. 2000). Hence, understanding the fate of seeds or other dispersed propagules placed into the environment is key to understanding population regeneration, plant distribution, and population genetics.

Once a seed leaves the parental plant, its movement to a germination site can be seen as the result of two phases in dispersal. Phase I (primary) dispersal is the

movement of a seed from the maternal plant to the ground by gravity (Watkinson 1978, Chambers and MacMahon 1994). This is characterized generally as short distance dispersal and has been well-documented in any number of species (Levin and Kerster 1974, Harper 1977, Willson 1993). The shape of primary seed distribution around a plant is usually leptokurtic (Willson and Traverster 2000) with the mode of the distribution very close to the maternal plant and seed density falling exponentially with distance beyond the mode. Phase II (secondary) dispersal is the movement of seeds after they have fallen to the ground (Watkinson 1978, Chambers and MacMahon 1994). This dispersal phase may be mediated by wind (Levin and Kerster 1974, Willson and Traverster 2000), animals (Stiles 2000, Christian 2001), rain splash (Reichman 1984), or water (Schneider and Sharitz 1988, Huiskes et al. 1995). Many seeds may not reach safe sites (sensu Harper 1977) during either primary or secondary dispersal. Nevertheless, because seeds move to a final germination site during the secondary phase of dispersal, it may be relatively more important than pri-

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mary dispersal in the patterns of plant distribution in some communities and ecosystems (Chambers and MacMahon 1994). The relative importance of secondary dispersal may be great when seeds are dispersed by animals (Stiles 2000, Willson and Traveset 2000) and/or moving water (Waser et al. 1982, Johansson and Nilsson 1993). For example, Skoglund (1990) found that water dispersal extends the dispersal distance of many species in a regularly flooded river.

The significance of seed dispersal by water has long been recognized (Ridley 1930), despite under-representation in some of the broader dispersal literature. For example, Harper (1977) made no mention of secondary seed dispersal by water, also called hydrochory. In their recent review of primary and secondary seed dispersal, Chambers and MacMahon (1994) did not discuss secondary seed dispersal by water, except for that due to transient water flow in rain runoff. Yet, seed buoyancy (Schneider and Sharitz 1988, Barrat-Segretain 1996), seed deposition patterns (Schneider and Sharitz 1988), and dispersal direction (Schneider and Sharitz 1988) may be critical to wetland plant regeneration. Wetland species often have special adaptations to prolong flotation of their seeds (Morton and Hogg 1989, Barrat-Segretain 1996). The seeds of a wetland species of *Asclepias* floated significantly longer than those of a non-wetland species (Edwards et al. 1994). Nevertheless, documented flotation times vary among wetland species. Seeds, sometimes with adhering flower or fruit parts (Barrat-Segretain 1996), float from a few hours to several months (Parker and Leck 1985, Schneider and Sharitz 1988, Smits et al. 1989, Edwards et al. 1994).

Differential flotation abilities among different plant species will affect seed deposition patterns and community structure in wetlands. Species with short and long floating times dispersed to different sites in a study by Nilsson et al. (1991). Species with seeds that floated for relatively short periods grew more often in standing vegetation compared to species with long flotation times, which remained in the seed bank (Grelsson and Nilsson 1991). Seed flotation interacted with germination and seedling survival over a moisture gradient to create zonation on riverbanks (Coops and van der Velde 1995). In contrast, seeds with different flotation abilities in a freshwater tidal wetland segregated equally to different zones of the wetland (Parker and Leck 1985).

Most studies of hydrochory have focused on seasonally flooded rivers or lakes (e.g., Schneider and Sharitz 1988, Skoglund 1990, Grelsson and Nilsson 1991, Nilsson et al. 1991, Johansson and Nilsson 1993, Gornall et al. 1998, Middleton 2000). These systems are characterized by a unidirectional flow of water. In contrast to seasonally flooded rivers, tidal sys-

tems flood twice daily, increasing the chance for seeds to disperse via water (e.g., Parker and Leck 1985, Leck and Simpson 1994, Huiskies et al. 1995). The daily ebb and flow of tides also removes constraints on dispersal that may be imposed by unidirectional flow. Huiskies et al. (1995) sampled seed dispersal in a tidal, salt water wetland and found differences among species in seed movement on the soil surface versus that of seed flotation on the water. They also found a net export of seeds on the tide, which was similar to the net export of floating taxa from a temporarily flooded river channel (Cellot et al. 1998).

In the work reported here, we focus on the primary and secondary dispersal of sensitive joint-vetch, *Aeschynomene virginica* L. (Fabaceae), a rare, freshwater tidal wetland annual. Seed dispersal research seldom combines primary and secondary dispersal (but see Schneider and Sharitz 1988, Middleton 2000), and one of our goals was to examine the relative importance of these dispersal processes in the dissemination of seed in *A. virginica*. We have seen only one other study of hydrochory in a rare, endemic plant (Cradock and Huenneke 1997), but the seed flotation experiments in that study had low replication. Because local population extinction represents a major threat to the prolonged existence of rare plants, seed dispersal into and out of localized populations is of special interest in these taxa. *Aeschynomene virginica* grows primarily along stream edges that are inundated twice daily by the tide. This streamside habitat suggests that secondary dispersal by water would be a major mechanism of seed dispersal in *A. virginica* because seeds may fall directly into stream flow or they may be moved by incoming or outgoing tides after falling to the ground.

We followed the fate of *A. virginica* seeds falling from maternal plants and moving on tidal water. We sought to investigate potential seed dispersal distances, as well as the potential impacts of this process on within patch population dynamics. Both population maintenance and the founding of new populations are important to the maintenance of rare and endangered plant species. As standing vegetation had significant impacts on other stages of *A. virginica*'s life cycle (Griffith and Forseth in press), we also manipulated standing vegetation to investigate the effects of vegetation on secondary dispersal. Specifically, we asked the following questions. 1) How far do seeds fall from the maternal plant? 2) How close do individuals of *A. virginica* grow to open/flowing water and are they close enough that some seed will fall directly into the water? 3) Does tidal inundation float seeds off the soil surface once they have fallen to the soil? 4) How long can seeds of *A. virginica* remain afloat on water? 5) Does standing vegetation alter seed movement from

the soil? 6) What is the potential dispersal distance of seeds by stream flow in the study area?

METHODS

We conducted this research on the Cumberland Marsh Preserve in New Kent County, Virginia, USA. *Aeschynomene virginica* grows in non-contiguous, patchily distributed populations along Holt's Creek and the Cumberland Thoroghfare, two tributaries of the Pamunkey River. *Aeschynomene virginica* most often grows along stream edges in areas of decreased standing vegetation on the levee or high marsh (U.S. Fish and Wildlife Service 1995, A. B. Griffith, personal observation). Twice daily tides inundate all sites of extant *A. virginica* populations, including our experimental sites. The removal of standing vegetation increases the establishment, survival, and reproduction of *A. virginica* (Griffith and Forseth in press). Thus, *A. virginica* may be a fugitive species (*sensu* Armstrong 1976) (i.e., a poor competitor that relies on dispersal to colonize disturbed and/or open habitat patches).

Aeschynomene virginica grows to heights of 1 to 2 m. Leaves are pinnately compound with 25–55 leaflets, each 1 to 2.5 cm long. Flowers grow in axillary racemes of 1 to 6 flowers, 1.0 to 1.5 cm long. Fruits are pods, 4- to 10-seeded (each 6 X 6 mm), which develop sutures between each seed. The pods easily break apart along suture lines at maturity (Brown and Brown 1984, U.S. Fish and Wildlife Service 1995). Generally, seeds disperse as single seeds enclosed within their pod segment during October and November (A. B. Griffith, personal observation).

Stratification is not a germination requirement of this species. Seeds break a physical dormancy after about five months in the soil. Seeds begin to germinate in late May or early June (Davidson and Bruderle 1984, Baskin and Baskin 1995), and germination rates are consistently 80% or greater for hard seeds (Baskin and Baskin 1995, A. B. Griffith, unpublished data). Seeds require moist to wet soil conditions and will germinate under flooded conditions (Baskin and Baskin 1995, A. B. Griffith, unpublished data). Germination and establishment of seedlings in the field is greater when vegetation is removed over *A. virginica* seeds sitting on the soil (Griffith and Forseth in press). In this research, any hard seed was considered viable.

We sampled seed fall from four isolated *A. virginica* plants on Holt's Creek. We constructed sticky seed traps (Werner 1975) with Tanglefoot® gel on circular paper disks about 113 cm² in area. The traps were placed in four 1.5-m-long radial transects. Each transect, except one on plant 2, contained six traps set at 0.25-m intervals starting as close to the stem as pos-

sible. One transect of traps had only three traps because the sloping creek bank made placement of more traps impossible. We raised each trap 53 cm above the soil surface in order to hold the seed traps just above the high tide level. Sampling seed fall above the soil surface underestimated the distance seeds fall from the plant if seeds fall at an angle away from the plant. However, raised traps also minimized the loss of seeds to tidal flows. Seeds in seed traps were counted every two weeks starting on 26 September, 1998, removed from the traps, and dropped to the ground below the trap. New sticky paper disks were added as necessary. Trap monitoring continued until the plant lodged naturally, or until 6 December 1998.

A dispersal experiment was designed to estimate the number of *A. virginica* seeds floating out of experimental plots and whether or not standing vegetation affects seed movement. We placed a single block of four treatment combinations at three different sites on the Cumberland Marsh during the summer and fall of 2000. We will refer to the sites by their relative positions on Holt's Creek, the downstream, midstream, and upstream sites. A distance of 0.25 km separated the downstream and midstream sites, and 1.0 km separated the midstream and upstream sites. Each 1.5 m² plot had a trapezoidal shape with the widest side placed towards the stream. We set up all experimental plots on the levee or high marsh at the edge of the stream bank. Nylon mesh screen (92 cm high and 1.7-mm mesh) surrounded all plots on the three sides away from the stream bank. On half of the plots, the mesh screen enclosed the fourth side, the side facing the stream bank, while the other half remained open on the fourth side. The top of the mesh screen was above high tides. In two of the four plots, we cut and removed all vegetation at the soil surface. Vegetation was recut at each seed count. In the other half of the plots, all vegetation remained standing. We randomly assigned the four treatment combinations to the four plots at each site. Forty *A. virginica* seeds, in their pods, were dropped into the center of each plot at low tide and left for one week. After this time, we searched each plot exhaustively, removed, and counted all seeds that were found. We replicated this experiment in time by placing seeds into plots 11 different times during the summer. A different fluorescent color distinguished the seeds from the different drop times. In order to maximize the number of replicates, we used seeds matured in the previous fall for the first seven seed drops and current season seeds in drops 8 through 11. Tests of seeds moving on the tide among these two groups of seed showed no significant differences due to age of seeds ($F_{1,59}=1.15$, $p=0.29$), so all seed ages were combined for subsequent analyses.

The distance of individual plants from the stream

edge was measured for 89 plants in 7 different populations on the Cumberland Marsh in September 1999. All plants in each population were measured. The distance was measured from the base of the plant stem to the nearest stream edge. The stream edge was defined as the stream bank where levee and upper marsh plants do not grow (Simpson et al. 1983).

Four stream stretches (signified A—D in Table 2) were chosen to estimate the flow rate of Holt's Creek. These stretches do not correspond to the dispersal experiment sites, but they do fall within the local distribution of *A. virginica* populations. We chose these stretches to capture variability in stream flow rates due to stream width and flow above and below a stream confluence. PVC pipes were used to mark a 10-m stretch of stream at each site. We measured the time it took an apple, thrown into the midstream flow to float the 10-m stretch of stream. The mean of two measurements at each sample time constituted the flow rate. We estimated both incoming tide flows (N=3) and outgoing tide flows (N=6).

Seed flotation times were estimated by filling ten plastic bowls (15 cm X 15 cm) with tap water and placing 25 mature seeds in each bowl. We counted the number of seeds floating in each bowl hourly between the hours of 8 am and 4 pm for nine consecutive days. We stirred seeds at each observation time to ensure that surface tension and adhesion to bowl sides did not keep seeds afloat.

Statistical Analyses

Initial analysis showed no differences in the number of seeds trapped among the four directions in which traps were placed ($F_{3,20} = 0.22$, $p = 0.88$). Therefore, we combined all seeds falling at a given distance from each isolated plant for further analyses. The area sampled by the sticky traps at each distance from the plant stem decreased with increasing distance. To adjust for this decrease in sampled area, we multiplied our seed counts by the total circular area in the distance interval of each set of traps. We regressed the natural log of this adjusted seed number (e.g., $\ln(\text{number of seeds} + 1)$) on the distance that seeds fell from the maternal plant. Regressions were done in PROC GLM (SAS Inc. 1996).

The closed plots in the dispersal experiment were intended to control for the seeds that remain hidden after searching experimental plots. The number of seeds not found in the closed treatments was subtracted from the open treatment of the same site, time, and vegetation treatment. Reusing each of the treatment plots in the factorial experiment introduced the possibility that the dependent variable (number of seeds retrieved in a plot) was not independent among the

times. Therefore, we used a mixed model with repeated measures to analyze our data. The model included VEGETATION (vegetation removed or left standing), SITE (downstream, midstream, or upstream site), TIME (one of 11 seed drop times) and all appropriate two- and three-way interactions. No interactions were significant, and they were subsequently dropped from the model. Model analysis was done in PROC MIXED (SAS Inc. 1996).

Our seed flotation data over time were highly skewed right and could not be made linear by a natural log transformation. The Weibull distribution is an asymmetric (skewed) distribution, which is also appropriate for censored data (i.e., seeds may remain floating at end of experiment). It has been used to estimate seed flotation over time (Edwards et al. 1994) and survivorship curves (Christensen 1984, Pyke and Thompson 1986, Dixon and Newman 1991). This distribution makes the proportion of floating seeds a function of time in the form:

$$p(\text{floating seeds}) = \exp[-(\alpha t)^\beta] \quad (1)$$

where β is a shape parameter, t is time, and α determines the location and spread of values in the distribution. β adjusts the probability of seeds sinking across time. For example, when $\beta=1$, the function is simply an exponential function, making the probability of seeds sinking constant over time. When $\beta<1$, the probability of seeds sinking increases over time, and when $\beta>1$, the probability of seeds sinking decreases over time (Dixon and Newman 1991).

We transformed equation 1 using the natural log to make a linear function in the form:

$$\ln(-\ln(p(\text{floating seeds}))) = b \ln(t) + a. \quad (2)$$

We used linear regression techniques to estimate the slope parameter b (the parameter estimate of β) and the intercept parameter a . Using the parameter estimates obtained from the regression equation 2, we calculated the time (t) during which different percentages of seeds remained afloat. For example, we calculated the times for 50 % of seeds still floating by using $\ln(-\ln(0.50)) = -0.366$. This was substituted into equation 2 and solved for $\ln(t)$. The antilog of $\ln(t)$ provided the estimates of absolute floating time. The standard error of $\ln(t)$ was obtained following Edwards et al. (1994) as

$$SE_{\ln(t)} = 1/b\sqrt{N} \quad (3)$$

where N is the number of observations used in the regression. Our experimental design was a repeated measures on each dish with seeds. Therefore, we used a mixed model with repeated measures analysis to estimate the slope and intercept. We used PROC

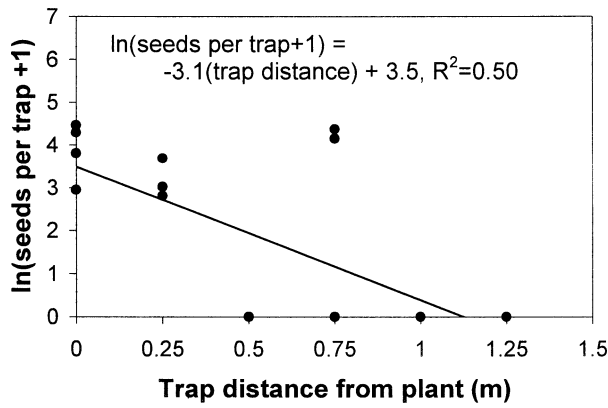


Figure 1. Number of seeds, natural log transformed, falling on traps at different distances from four isolated *Aeschynomene virginica* plants. The numbers falling at each distance are corrected for the increasing unsampled area with distance from the plant.

MIXED (SAS Inc. 1996) for these mixed model analyses.

RESULTS

The number of seeds falling onto seed traps decreased rapidly with increasing distance from maternal plants (Figure 1). Of the 148 seeds caught in the seed traps, 94% of the seeds fell within 0.5 m of the maternal plant stem. No seeds were found on traps 1 m or more distant from the maternal plant. The slope and intercept of the log linear regression ($R^2=0.50$) of seed number per trap and trap distance from plant were significant ($p<0.0001$), the slope was -3.1 ± 0.7 (± 1 SE), and the intercept was 3.5 ± 0.5 (± 1 SE). The variability of the adjusted number of seeds falling at each distance increased with the distance from the plant (Figure 1). At 0.75 m from the plant, traps at two of the replicate plants had no seeds and traps at the other two plants had 4 and 5 seeds or 62 and 74 seeds when adjusted for sample size.

The main effects of VEGETATION and SITE in the secondary dispersal experiment were not significant, while the TIME that seeds were dropped into the plot

Table 1. Mixed model results for number of seeds retrieved from plots one week after they had been dropped into the plot. VEGETATION is vegetation cut or uncut in plots. SITE is one of the three sites on the stream, and TIME is one of eleven different seed drops.

Source of Variation	DF (ndf, ddf)	F-Value	p-Value
VEGETATION	1, 2	1.41	0.3566
SITE	2, 2	0.015	0.8677
TIME	10, 50	2.74	0.0091

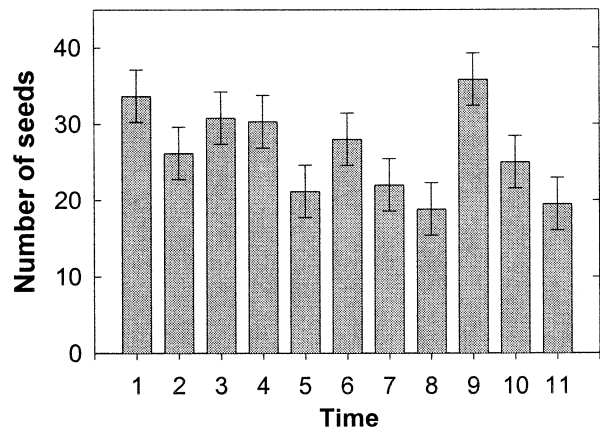


Figure 2. Mean number of seeds (± 1 SE) recovered (out of forty that were dropped) from dispersal experiment at 11 sample times. Each value is the mean of two treatments and three sites. There were significant differences in the number of seeds recovered among the 11 sample times.

was significant (Table 1). We retrieved an average of 26.5 ± 5.8 (± 1 SE) seeds at each time. The percent of the original seeds that were not retrieved varied from 11% to 53%. There was no consistent trend across the 11 collection times (Figure 2).

Aeschynomene virginica seeds do not wet quickly when dropped in water (A. B. Griffith, personal observation), and this could partly account for their ability to float. The parameter estimates of equation 2 are significantly different from 0: $b = 1.43 \pm 0.02$ (± 1 SE, $p<0.0001$) and $a = -5.11 \pm 0.11$ (± 1 SE, $p<0.0001$). The percentage of seeds floating fell steadily over the first three days that seeds were in water, resulting in 50% of the seeds still floating after 28.4 ± 1.2 hours (± 1 SE), 25% of the seeds floating after 46.7 ± 1.2 hours (± 1 SE), and 5% of seeds floating after 81.8 ± 1.2 hours (± 1 SE) (Figure 3). One seed in one pan remained floating up to nine days after the beginning of the experiment.

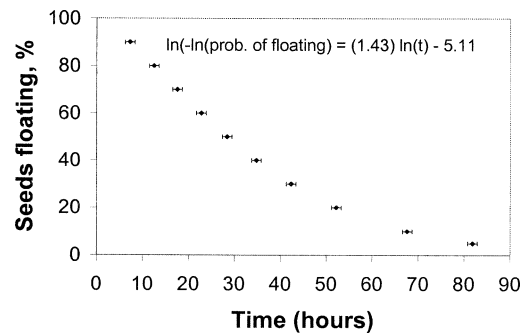


Figure 3. Percent of *Aeschynomene virginica* seeds still floating over time. Time is hours after seeds were dropped into water. Time (± 1 SE) to which percentage of seeds floated was calculated from equation shown.

Table 2. Water flow rates (± 1 SE) and estimated travel distance (± 1 SE), on the incoming and outgoing tide, of objects in the stream adjacent to *Aeschynomene virginica* L. populations. Sample size is $N = 6$ for the incoming tide and $N = 3$ for the outgoing tide.

Flow Direction	Site	Flow Rate (m/s)	Distance Traveled in 4 Hours (m)	Mean Distance for Flow Direction (m)
Incoming tide	A	0.28 ± 0.07	3711	2694 ± 1024
	B	0.15 ± 0.07	1371	
	C	0.17 ± 0.05	2449	
	D	0.24 ± 0.06	3243	
Outgoing tide	A	0.28 ± 0.08	3750	2903 ± 671
	B	0.18 ± 0.11	2111	
	C	0.21 ± 0.03	2927	
	D	0.20 ± 0.02	2824	

Water flow rates taken at four different sites along the stream varied greatly. The range of times it took an apple to float 10 m was 66 s during incoming tides and 30 s during outgoing tides. The mean flow rates were greater for the outgoing tide than the incoming tide at two of four sites. The third site had equal rates for the outgoing and incoming tides and the fourth had a slower flow rate for the incoming tide (Table 2). The estimated mean distance an object could float in a 4-hour tidal cycle was 2903 ± 671 m (± 1 SE) on the outgoing tide and 2694 ± 1024 m (± 1 SE) on the incoming tide. These distances were not significantly different (one sided paired t-test, $p=0.24$).

The number of plants in the populations, in which distance to stream edge was measured, ranged from 2 to 48 plants, and the distance between adjacent populations ranged from 10 m to 2500 m. The mean distance between adjacent populations was 348 m. The majority, 59.6%, of plants in extant populations were located greater than 1.25 m from the stream edge (Figure 4). Nevertheless, over 33% of the plants were located within 1 m of the stream edge, and 10.1% were within 0.5 m of the stream edge. The average distance measured on the 89 surveyed plants was 1.5 ± 0.87 m (± 1 SE). The median distance was 0.9 m.

DISCUSSION

The floating abilities of the seeds of *A. virginica*, combined with its stream edge habit, stream flow estimates, and twice daily tidal inundation, suggest a significant potential for secondary dispersal by water of seeds in this species. Seeds falling from *A. virginica* can leave population patches and enter adjacent streams by different processes; seeds may fall directly into the stream or tidal currents can lift seeds from the soil and carry them into the stream. Secondary dis-

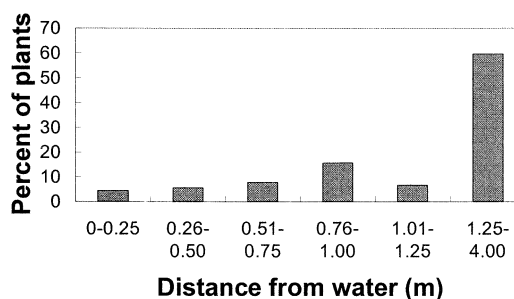


Figure 4. Distance of *Aeschynomene virginica* plants from the water's edge. Eighty-nine plants in seven populations were measured.

persal may represent an important mechanism for a fugitive species, such as *A. virginica*, that specializes in open, disturbed habitats to find and colonize habitat patches.

The majority of *A. virginica* seeds fall very close to the maternal plant, as expected. *Aeschynomene virginica* seed pods are large and have no specialized wings or appendages to extend wind dispersal as they fall to the ground. The size of *A. virginica* seeds and their lack of adaptations for wind dispersal probably minimize the influence of the wind on seed fall. Herbaceous species consistently show a quick drop off in the distance seeds fall from the plant (Willson 1993), particularly when seeds show no special structures for dispersal (McCanny and Cavers 1987).

There are two reasons why short primary seed dispersal distances would still be sufficient to deposit a significant percentage of seeds directly into the water. The first is that all plants in the populations that we studied will drop seeds directly into the water at high tide. The second is that many plants stand within a short distance of flowing water when high tides are not present. During one season, 10.1% of *A. virginica* stems were within 0.5 m of flowing water (Figure 4). Plants close to the stream edge would be more likely to deposit seeds directly into the water at low tide. Their seeds are thus more likely to be transported longer distances than seeds falling directly to the ground. Other plants living on or near stream edges drop their seeds directly into the water. *Taxodium distichum* (L.) Rich. (Schneider and Sharitz 1988, Middleton 2000) and *Nyssa aquatica* L. (Schneider and Sharitz 1988) seeds fell directly into the water during high water periods and moved away from the place of initial seed deposition.

Aeschynomene virginica seeds that fall to the soil are still likely to be moved by tidal flows. Our results suggest that 34% of seeds that drop into stream edge patches leave those patches on the tide, but this percentage varied between 11 and 53%. The number of seeds leaving stream edge patches varied from week-

to-week (Figure 2) with no discernible pattern. Freshwater tidal wetlands develop between the influences of tidal forces downstream and freshwater flows from upstream (Odum 1988, Mitsch and Gooselink 1993). These influences combine to vary stream flow and height from week to week. The variation of stream height and velocity could lead to variation in the number of seeds leaving stream edges as more seeds can be physically dislodged by higher water levels and velocities (Parker and Leck 1985, Leck and Simpson 1994). This week-to-week variability suggests that the timing of seed fall from a plant could affect its potential dispersal distance. Seasonal flooding, from hurricanes moving up the U.S. East Coast can influence both tidal fluctuations and downstream flows. The official hurricane season is June through November, which overlaps the seed dispersal period of *A. virginica*. It is not clear how these periodic extreme events would affect seed dispersal, but these conditions would be quite different from those in our experiment.

Whether seeds fall directly into water or are moved by the tide, seed movement by water is potentially important to the population dynamics of *A. virginica* in at least two ways. First, seed movement out of patches may impact population dynamics of the patch from which the seeds leave. The effects on population dynamics within a patch would be similar to the effects from seed or seedling death of seeds that did not disperse from the patch. Seeds that die or emigrate from a patch cannot contribute to the population in that patch the following season. Seed emigration will have a stronger impact on populations when they are isolated. Isolated populations are less likely to receive immigrating seeds from adjacent populations that would balance the emigrating seed loss (Watkinson 1978). Seed emigration would also have stronger impacts on small populations (e.g., 1 or 2 individuals). The combination of seed emigration and seed death may place small populations at greater risk of extinction due to demographic stochasticity (Richter-Dyn and Goel 1972, Leigh 1981).

Second, seed dispersal may be a significant pathway to demographically connect populations in a metapopulation (Cain et al. 2000). Seed dispersal may result in the recolonization of a suitable habitat patch after a localized population extinction (Husband and Barrett 1996), it may rescue a population from extinction (Brown and Kodric-Brown 1977), or it may augment a population's size (Watkinson 1978). Seed dispersal has been invoked as an important mechanism for population regeneration in other annuals of freshwater tidal wetlands like *Amaranthus cannabinus* (L.) Sauer., *Cuscuta gronovii* Willd., and *Juncus effusus* L. (Leck and Simpson 1994), although direct measurements of dispersal have not been reported for these species. Rel-

atively few studies have attempted to measure hydrochory in tidal systems (but see Kudoh and Whigham 1997, 2001). Seeds of plants in a salt water marsh were found to move on both the incoming and outgoing tide, but these movements were species-specific (Huiskes et al. 1995).

Long-distance water dispersal also has the potential to affect the distribution of genetic variability within and between populations of *A. virginica*. Dispersal resulting in a well-mixed seed pool may reduce genetic variability, while less homogeneous dispersal may increase genetic diversity. At the present time, we have no specific data as to which case predominates in the extant populations of *A. virginica*. However, *A. virginica* seed flotation time suggests that seed dispersal may connect disjunct populations. Seeds can float up to nine days, but the majority of seeds float only one day, a short time relative to other wetland plants. For many wetland species, as many as 50% of their seeds float at least five days, and plants like *Bidens laevis* (L.) BSP. and *Impatiens capensis* Meerb. have more than 40% of their seeds floating after 30 days (Parker and Leck 1985). Nevertheless, these relatively short flotation times are sufficient to move floating seeds a considerable distance. Mean flow rates during a 4-hour incoming or outgoing tidal cycle may move a floating seed over 2600 m upstream or downstream. This is a potential maximum distance, since floating seeds often become lodged among streamside vegetation and other emergent objects (Schneider and Sharitz 1988, Nilsson et al. 1991). However, this dispersal potential is on the order of the current range of known *A. virginica* populations in Virginia. Seed exchange would certainly be likely to take place between adjacent populations due to the short flotation times.

The presence or absence of standing vegetation around *A. virginica* plants had significant impacts on seedling establishment, seedling survival to reproduction, and seed set (Griffith and Forseth in press). However, we did not find any effect of vegetation removal on secondary seed dispersal by the tide. Similar numbers of seeds left all plots. These seeds were transported into the stream on tidal water movement and not into the marsh behind plots, as screens barred movement in that direction. These results contrast to seed movement in some non-wetland systems. On sand dunes, more seeds moved away from their initial landing place as vegetation cover decreased (Watkinson 1978). Seeds became stranded in patches of bryophytes in chalk grasslands, leading to greater dispersal in the absence of bryophyte cover (van Tooren 1988). Seeds in other tidal systems moved freely on tidal currents and seed movement was not affected by different stem densities (Kudoh and Whigham 1997).

In conclusion, secondary seed dispersal by tidal

flows has the potential to disperse seeds of *A. virginica* throughout the tidal marsh system where it currently occurs. This seed dispersal may play a significant role in the metapopulation dynamics of this population, serving to disperse seeds to new suitable habitat patches and connecting source with sink populations. Since *A. virginica* performs poorly in habitats with established conspecifics, dispersal to open sites may be a key process in maintaining its presence in the tidal wetland plant community.

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LITERATURE CITED

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